ON THE VARIATION OF THE SHELL OF PECTEN IRRADIANS LAMARCK FROM LONG ISLAND.

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THIS study is concerned with the shells of the prevalent species of scallop, *Pecten irradians*,[1] from Cold Spring Harbor, Cutchogue, Fire Island Beach, and Oak Island Beach, Long Island, state of New York, collected during August and September, 1899.

Pecten (Fig. 1) is a genus of bivalve Mollusca whose nearly circular valves are provided with a number of ridges radiating from the beak at the hinge. The hinge is elongated tangentially, forming a pair of "ears" where the ends of the tangent depart most widely from the circle. The ears of the two valves are very different, as, indeed, are the conditions to which the two valves are subjected in nature. For when Pecten is about three millimeters in diameter it attaches itself, so that it lies in a horizontal fashion, by means of a byssus. It remains attached until it is from ten to thirty millimeters long, after which it lives free. The byssus passes to the exterior between the anterior ear of the right valve and the main body of the shell ; consequently, when the right valve is viewed exteriorly, the right-hand ear is deeply notched,[2] while the left-hand ear is not notched at all. In the left valve both

[1] As it is necessary nowadays to recognize that a specific name by itself means very little, a string of synonymy must be appended. Recent names for the "species" or "variety" to which the form-units that I studied belong, are : *Pecten* (*Plagioctenium*) *gibbus*, var. *irradians* (Dall, **'98**, p. 748), and *Chlamys* (*Æquipecten*) *irradians* (Verrill, **'99**, p. 77). Dall recognizes two northern varieties of gibbus : "gibbus var. borealis" of the New England coast, and "gibbus var. irradians" "from New Jersey" south. Neither of his descriptions of these two forms agrees closely with the Cold Spring Harbor form-unit, which might therefore receive a new varietal name were not the futility of this endless naming, alas, too evident.

[2] Fig. 1, top.

ears are unnotched.[1] Since the byssus passes out on the right side, the right side of the young Pecten lies next the substratum, while the left side is broadly exposed to the water above. I was interested to see whether the Pecten ever lies on its left side — a condition which would be comparable in a way

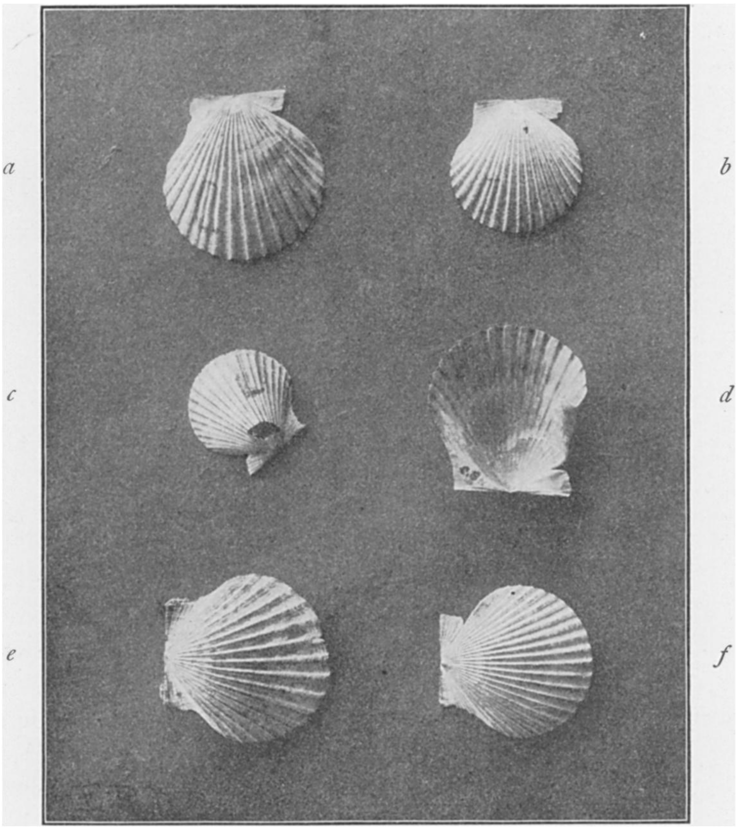

FIG. 1. — Photographs of *Pecten irradians* from Cold Spring Harbor : *a*, *b*, two cases of partial division of a rib; *c*, case of interpolation of a secondary ridge between two primary ones; *e*, *f*, showing an extremely small (14) and extremely large (20) number of rays.

with left-handedness in dextral gastropods. If the abnormal condition ever occurs, it will show itself by the circumstance that the notch will appear on the left side of the valve, viewed exteriorly. Now, although over a thousand notched shells

[1] Fig. 1, bottom, left.

were examined by me, I found no exception to the condition of being notched on the right ear. Jackson ('90) found no exception to the normal condition, and states that Professor Hyatt examined over three hundred specimens of *P. irradians*, all of which lay on the right side. There is, accordingly, a wonderful constancy in the tendency to lie on the right side; and this tendency is characteristic of many related genera, such as Pinna, Spondylus, Plicatula, Hinnites, and Anomia. The constancy in the position of the notch is referable to a constancy in the position of the byssus gland. This is normally laid down in development as a pair of glands, right and left. Apparently only the right gland persists, or else perhaps both glands are united on the right side. Whatever the morphogenetic process which determines the position of the byssus gland, it is a remarkably constant one.

The shell of *P. irradians* exhibits on its outer surface five areas: First, a middle one, characterized by large prominent ridges, alternating with furrows. Since these are made by foldings of the mantle, the outer ridges appear as grooves on the inner surface, and the outer grooves as inner ridges. Second, a pair of "ear" areas characterized by fine linear elevations which do not correspond with marked grooves on the inner face. Third, a pair of triangular areas, lying between the middle areas and the ear areas, and transitional between them. These may be called the "transition" areas. They bear indistinct radial thickenings. These areas are bounded laterally by the ear areas. On the right, or notched, side of the right valve the boundary is distinct; on the left side of the right valve and on both sides of the left valve the lateral limit of the transitional area is determined by the line where the ear begins. But this is not a very precise line. The transitional areas are bounded mesially by the middle area. The limit may be defined as the line where an internal groove corresponding to an external ridge first appears. Since the external ridges on the shell are so often obscure, I early abandoned the attempt to count them. I then noticed that the internal grooves are much more precise than external ridges;

so I counted these grooves to get the laws of variation in the number of radii in Pecten. Such a study is of some importance, because the valves on which the series occur are not typically symmetrical, but show a certain tendency towards being dorsal and ventral. We have here, then, a case among pelecypods resembling that of the flounder among fishes.

The grooves in all the shells examined ran continuously from near the beak to the free margin of the shell. I did not observe any case of bifurcation of a groove, the obliteration of a groove distally, or the introduction of a new groove towards the free margin of the shell. This is the more remarkable because in allied species, such as *P. eboreus* Conrad (see Dall, '98, p. 749), some of the ribs become obsolete toward the margin, and in others, as *P. islandicus*, new grooves are begun at various stages in development of the shell.

The number of grooves corresponds to the number of ridges in the "middle" area. But the number of grooves on the inner face of the shell is not always definite, especially towards the transition area. We here sometimes find a very slight lateral depression passing hinge-ward only one-tenth to one-fifth the whole distance. The rule was adopted to count as grooves only those depressions where the margin of the shell was folded to form a complete U rather than merely an L. A strictly ambiguous or halfway groove at both ends of the series counted for one full groove, but when only one groove was ambiguous, that was omitted from the count. About ten per cent of the shells from Cold Spring Harbor and all from the other two localities were counted by my wife, Gertrude C. Davenport; the rest were counted by myself. We satisfied ourselves of the equivalence of our estimates of doubtful cases by making a series of independent determinations on a number of identical shells, finding that we agreed in our determinations in the case of each individual shell.

The shells from Cold Spring Harbor were picked up on the sand spit, where they had been thrown by waves and shifting sands. They were therefore not pairs, and were not consciously selected. The shells from Fire and Oak Island Beaches were picked up on the beach and were also separate and

often somewhat water-worn and broken by the pounding of the surf which rolls in on that unprotected shore; but no shells were rejected unless so worn or broken as to obscure the grooves. The shells from Cutchogue were very kindly sent me by Mr. Huron Bretsch. Mr. Bretsch writes me that all came from Peconic Bay, near Cutchogue, some from a shell heap left by fishermen, and some picked up on the shore by himself. He says, "I did not pick out the best ones, but took them at random."

Results. — I give in tabular form the observed and per mille distribution of frequencies of the different classes of groove numbers for the two valves from the three localities.

Classes	Right (Lower) Valve						Left (Upper) Valve					
	C. S. H.		Cutchogue		F. I. & O. I.		C. S. H.		Cutchogue		F. I. & O. I.	
	Obs.	P.M.	Obs.	P.M.	Obs.	P.M.	Obs.	P.M.	Obs.	P.M.	Obs.	P.M.
13							1	1.2				
14	2	1.9			1	20	2	2.5	5	32.7	2	95.2
15	15	14.3	33	117.4	6	120	43	53.2	38	248.4	4	190.5
16	108	103.3	95	338.1	15	300	269	333.0	77	503.2	10	476.2
17	515	492.3	127	452.0	24	480	320	396.0	27	176.5	4	190.5
18	308	294.5	22	78.3	4	80	151	186.9	4	26.1	1	47.6
19	90	86.0	4	14.2			22	27.2	2	13.1		
20	7	6.7										
21	1	1.0										
	1046	1000.0	281	1000.0	50	1000	808	1000.0	153	1000.0	21	1000.0

The quantitative study of these seriations gives the following constants calculated from the observed and not the per mille data. Here n is the number of individual shells counted; M is the *mode*, or the prevailing number of rays; A is the average number of rays; σ is the standard deviation or index of variation; c is the coefficient of variation; F is the critical function of Pearson, by which the type of the curve is determined. The numbers following the $\pm$ sign are the probable errors of the determinations. For further information concerning this analysis of frequency distributions, the reader is referred to the works of Duncker in *Roux's Archiv*, 1899, or my *Statistical Methods*, New York, 1899.

	Right (Lower) Valve			Left (Upper) Valve		
	C. S. H.	Cutchogue	F. I. & O. I.	C. S. H.	Cutchogue	F.I.& O.I.
n	1046	281	50	808	153	21
M	17	17	17	17	16	16
A	17.353 ± .018	16.534 ± .034	16.480 ± .084	16.790 ± .022	15.954 ± .105	15.90 ± .14
σ	0.876 ± .013	0.852 ± .024	0.877 ± .060	0.916 ± .015	0.881 ± .075	0.97 ± .10
c	5.049 ± .074	5.15 ± .15	5.32 ± .36	5.457 ± .092	5.52 ± .47	6.11 ± .64
F	— 1.46			— 0.0476		
Type	IV			Type IV or Type V [1]		
Skewness	+ 0.023			+ .000000058		

[1] $F \times \mu_2^3 = .028$; $\dfrac{3\,\nu_2^2 - 2\,\nu_1^4}{\nu_4} = .9711$.

Conclusions. — From these numerical results we may draw the following conclusions:

1. The right valve has on the average about half a groove more than the upper valve (more precisely .56+ more). This result is due to the circumstance that the series of ridges and grooves must end either in a ridge or in a groove. Of course it may end in a ridge at one end of the series and a groove at the other; but in the majority of cases there is a high degree of symmetry in the ends of the series. Now I find, in looking over the right and left shells without prejudice, that in the right shells the series tends strongly to end in a groove, so that the last or most lateral ridges of the series (looking at inner surface of shell) are very distinct. In the left valve, on the other hand, there is a more marked tendency for the series to end in a ridge, so that the last grooves are distinct. For in twenty-three right valves I found only three in which the series ended in ridges, whereas twenty ended in grooves; whilst in twenty-nine left valves in fourteen cases the series ended in ridges, and in fifteen cases in grooves.[1] Since the series of the right valve show this prevailing tendency to end in grooves, the excess of grooves on the right valves is fully accounted for. Doubtless if ridges had been counted instead of grooves, the right valve would have averaged one-half a ridge less than the left.

[1] The tendency to end in a groove or a ridge is beautifully shown in *P. operculatus* Linn.

2. The prevailing number of rays in the right valves from all localities is seventeen; in the left valves from Cold Spring Harbor it is seventeen also; but at the east end and the south shore of Long Island it is sixteen. Comparison of the averages shows that the Cold Spring Harbor shells tend to have a comparatively large number of rays on both valves — in the mean 0.8 of a valve more than in the other localities. In the average number of grooves Cold Spring Harbor stands widely separated from the other two localities, which are closely related.

3. Using as an index of variability the standard deviation σ, it appears that the Cold Spring Harbor shells are possibly more variable than those from Cutchogue. However, the difference is less than the probable error, and no stress is to be laid on the fact. The same is true of the apparently greater variation of the South Shore shells. So we may conclude that, despite differences in the mean, the variability of the grooves is constant. This result accords with certain others obtained by *counting integral variates.* Duncker ('99, p. 328) says: "While the average values of a character may differ widely in different form-units of the same species, the indices of variability remain fairly constant, not only in the form-units of the same species, but also in those of species belonging to different genera, even to different families. This fact does not seem to me to have been sufficiently regarded hitherto; the explanation of it is, I suppose, the constancy of the physiological capacity of a given organ for reacting to the individual causes of variation . . . with respect to a given character. Some authors, however, seem to assume a more or less constant relation between the height of the average and that of the index of variability of a character." I will not here discuss, as I propose to do elsewhere, the relation between the mean and the index of variation. The matter needs special investigation.

4. The variability of the right or lower valve is in every case less than that of the left or upper valve, and this difference in the case of the Cold Spring Harbor specimens is greater than the probable error. From this fact we may conclude that the right valve is the more conservative, or responds less to

varying environmental conditions. This small variability of the lower valve is in accord with the fact that the young shell of Pecten is larger and better preserved on the right valve than on the left. Again, in *P. squamosus*,[1] in which the scales are becoming obsolete in the adult, they are found at a later stage on the right valve than on the left. In other cases,[2] the grooves of the left valve divide and become ornamented, while the right valve remains simple. Here, then, the index of variability is an index of phylogenetic changeableness.

5. The type of distribution of frequencies was determined only for the shells from Cold Spring Harbor, because they alone were sufficiently numerous for this purpose. The right valve is Type IV, with a rather small skewness however, namely, +0.023. For the left valve the distribution is remarkably near the theoretical normal distribution, the skewness being +.0000000058. The skewness will rarely be theoretically zero. Applying Pearson's limits, the distribution may be said to be of the normal type. Applying the prevailing method of interpreting these results, we may say that the Cold Spring Harbor race is, as regards the grooves in the upper valve, very stable; while as regards the grooves in the lower valve it exhibits a slight tendency to the excessive production of a large number of rays, or to the selective annihilation of the small numbers. The excessive production of large numbers may be due to innate or to external causes.

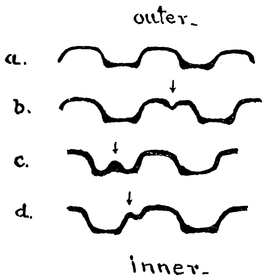

FIG. 2.— Cross-Sections of the shell of *Pecten irradians* (outer surface uppermost); *a*, normal; *b*, a double ridge; *c*, a double groove; *d*, a lateral groove.

Abnormalities of the grooves often occur. All gradations were found between the condition of a broad ridge on the inner face of the shell and the condition of a double ridge, the halves of which were separated by a groove (Figs. 1, *a*, *b*; 2, *b*). In other cases the groove contains a ridge of varying size (Figs. 1, *c*; 2, *c*). Occasionally a small groove

[1] From Mauritius, No. 2412, Field Columbian Museum.

[2] For instance, *Pecten madreporium*, from Singapore, No. 6109, Field Columbian Museum.

lies close by the side of one of normal size (Fig. 2, *d*). All these abnormalities may be regarded as congenital. In addition I have found certain variations, probably due to injury of the mantle. Jackson ('90) remarks that the mantle is subject to injury by fish and thereafter regenerates only imperfectly. He accounts for the incurved edge of the shell which is occasionally found (Fig. 1, *d*) as follows: "When one mantle border is injured, the other repairs the damage which would be caused by local want of shell growth, by curving the shell deposition of the injured side rapidly inwards, thus obviating the deficiency of the injured area. This ingrowth is probably induced by the lack of resisting support on the part of the damaged border."

We have now to consider the question whether the individual variations and the abnormalities which we have studied throw any light on the question of the origin of species in the Pectinidæ. This involves an examination of the genus Pecten.[1]

This genus has been variously subdivided. The subgenus Chlamys (as defined by Dall, '90, p. 695), which includes *P. irradians*, is a fairly well defined subdivision, and our attention may be confined to it. The species all have "ribs," as I shall designate the alternating ridges and furrows, which are true flutings or corrugations affecting both inner and outer surfaces of the shell. If the ribs are absent in any case, they have secondarily become lost. The valves are nearly equally inflated; the ears vary from a nearly equal condition to one of great inequality. The anterior ear of the right valve is typically notched, to let pass the byssus. In judging of the position of *P. irradians* we need to know something of the phylogeny of the subgenus Chlamys. We can infer something, as Jackson ('90) has, on the recapitulation hypothesis, by noting the condition of the shell at different stages of development. The record of these changes remains in the adult shell, and can be studied by examining the beak and adjacent parts. Fossil remains also tell something. The beak

[1] In making this examination I have had the great privilege of examining, with the kind assistance of Dr. S. E. Meek of the Field Columbian Museum, the very fine collection of Pectens possessed by that institution.

of the valves, especially the *right* valve, shows an area without striations; at this stage also the hinge is as long as the greatest diameter of the shell, and there are no sharply marked off "ears." At this stage the shell resembles the Devonian Aviculoids, which are usually regarded from this as well as from paleontological evidence as the ancestors of the Pectinidæ. The genus Pecten began to emerge in the Devonian and Carboniferous. These emerging Pectens, Pterinopecten (Devonian), had a long hinge line, with large, not sharply defined, nearly equal ears, and with a byssal sinus on the right valve. Both the valves seem to have been convex. Jackson ('90, p. 386) says that *Pterinopecten dignatus* Hall and other species bear a close resemblance to the young of *P. irradians*. In Aviculopecten (Devonian), which represents another step towards Pecten, we see the hinge becoming shorter and the two ears well defined; a deep byssal sinus occurs on the right valve in many species. In both Pterinopecten and Aviculopecten the shell is corrugated. These dawning Pectens then had the characters of the subgenus Chlamys, which may consequently be regarded as the most primitive of the subgenera of Pecten. *P. irradians*, therefore, belongs to the most primitive division of the genus Pecten.

Inside the subgenus Chlamys the species show modifications in various directions. There are species in which the posterior ear has become very much smaller relatively than in irradians; *e.g.*, islandicus of our coast, hericeus (= hastatus) of the California coast and Vancouver, and niveus of Great Britain. Associated with this diminution in the posterior ear is the formation of scales in a linear series on the ribs. The scaled condition is secondary, as is clearly shown in niveus, where the younger shell is without scales;[1] the scales are obtained only in the later stages. The inequality of the ears is also derived, for in the primitive condition there was equality of the auricles.[2] This group is therefore more modified than *P. irradians*.

[1] The scales appear earlier on the lower than on the upper shell.

[2] It is interesting that in certain species, *e.g.*, *P. squamosus* of Mauritius, the scales seem to be secondarily disappearing. This species would seem to have originated from an ancestor resembling *P. hericeus*.

A second class of modifications consists in the formation of striations on the ribs. These striations are thickenings of the shell in radial lines. They may in some cases become so pronounced as to form ribs at the periphery of the shell. These striations I regard as secondary, both because they are clearly something added to the simple rays which we have in Pecten, because the young stages of Pecten show no such striations, and because in the young stages of striated shells the striæ are absent. Consequently these striated species are more modified than irradians.

A third class of modifications is that of smooth or nearly smooth shells. Of this condition our *P. magellanicus* (= clintonius) is typical. Although the ancestors of Pecten were smooth-shelled, the magellanicus modification is by no means ancestral, for if, as Verrill (**'99**, p. 78) states, "when about 3–4 mm. in length it develops small, regular, raised ribs over the whole surface of the upper valve and usually at both ends of the lower one," this shell must have been derived from ribbed ancestors. So, too, in *P. glaber* of Smyrna and *P. danicus* of Scotland we have the process of obliteration of ribs going on with the formation, apparently, of a few large secondary crenations.[1] In all cases we start with a ribbed form like irradians.

Let us consider, finally, the relation of irradians to the other species of Chlamys in respect to the number of ribs. The data for such a comparison can be got from an important lot of countings made by Dall (**'98**) and from some determinations of my own made on shells in the collection of the Field Columbian Museum. I give only modes (or, in the absence of sufficient data, the ranges) for the *left* valve. In some cases external ridges are given because these are often alone available and Dall has counted ridges only. In other cases I give internal grooves ; these are exclusively derived from my countings. Since the extreme lateral external ridges usually have no internal grooves, the groove numbers run one or two lower than the ridge numbers.

[1] An insufficient amount of material requires me to put forward this explanation with some reserve.

		Ridges.	Grooves.
P. nodosus,	Southeastern North America . .	7–10	
P. jeffersonius,	Miocene fossils, S. E. North America .		
	var. septenarius	8	
	var. Jeffersonius	10	
	var. edgecombensis	14	
P. latiauratus,	var. monotimeris, California . .		12
P. pallium,	Pacific Islands		13
P. madisonius,	precursor of *P. jeffersonius*, fossil .	15	
P. gibbus,	var. amplicostatus	16	
	var. borealis, recent	17	
	from New England, irradians . .		16
	" South Shore, L. I., irradians .		16
	" Cold Spring Harbor, L. I., irradians		17
	var. irradians, recent	19	
	" " fossil, late Pliocene .	19–22	
	var. dislocatus, fossil, late Pliocene .	18	
	" " recent	20	
P. eboreus,	precursor of *P. gibbus* (= irradians) Miocene and Pliocene	22	
P. operculatus,	British		18
P. hericeus,	Vancouver		19
P. varius,	Naples		24

From this table it appears that *P.* (*gibbus*) *irradians* is intermediate in the number of its ribs between the extremes. The question arises whether in phylogeny the number of rays has been increasing or decreasing to produce *P. irradians*. From the data given and on the assumption that *P. eboreus* is the ancestor of *P. irradians* we have the series :

P. eboreus, Miocene and Pliocene	22 ribs.
P. irradians, late Pliocene	22–19 ribs.
P. irradians, recent	19 ribs.

This seems to indicate that there has been a tendency for the number of ribs slightly to decline. On the other hand, the fossil *P. gibbus*, var. dislocatus (the southern form of irradians), shows an increase from eighteen to twenty ribs in passing from the late Pliocene to the present. Also, the more specialized species, such as varius, twenty-four rays; striatus, fifty-one rays; miniaceus (South Africa), thirty to forty rays; and islandicus (east coast, United States), thirty-five to fifty rays,—

tend to larger numbers than irradians. In many of these cases of species, with a larger number of rays at the periphery, there is an ontogenetic increase. Thus the epionic shell of miniaceus has only sixteen rays, and the left valve of islandicus has only nineteen ridges at 5 mm. from the beak. These species, then, judging from ontogenetic changes, have been derived from species with fewer rays, such as we find in irradians. Finally, Dall ('98, p. 748) concludes in respect to *P. gibbus* (= irradians in part): "Taking all varieties together, the generalization may fairly be made that in the Pliocene the proportion of specimens with less than nineteen ribs is decidedly larger than among recent shells." The apparent contradiction between this statement and the figures which Dall gives for the number of rays in fossil groups suggests that the figures are based on too few individuals to be significant. It may be concluded, consequently, that the condition of about eighteen rays exhibited by *P. irradians* is not far removed from the ancestral condition, and that most of the species with numerous rays have been derived from forms which, like irradians, have fewer than twenty rays.[1]

These facts have a close relation to those of individual variation in our form-unit of *P. irradians*. First, the number of ribs, which is so variable in the individuals of the form-unit studied, is likewise very different in the different species of the genus.

Again, as we have seen, the asymmetry of groove frequencies in *P. irradians* is in the positive sense; that is, there is a tendency to an excess of rays; in other words, there is a tendency to vary in the direction of *P. islandicus;* to go the path that it has trod.

[1] I have paid some attention to the ways in which the increase in rays is brought about in the different species. In islandicus the nineteen rays at the beak increase in the left valve to forty, chiefly by the interpolation of new ridges in the old furrows. Such interpolated ridges start at various stages. In the older shells the increase is also effected by bifurcation of certain of the larger ribs, of which there are about six to eight. In the right valve, on the other hand, the ribs increase chiefly by bifurcation, although interpolations also occur. I have observed the same difference between the left and right valves in other species; namely, *P. alvolineatus* Sby., from Viti (Field Columbian Museum, No. 6111); *P. tigrinus* Müll., from Great Britain (Field Columbian Museum, No. 6118); and *P. madreporarium* Petit, from Singapore (Field Columbian Museum, No. 6109).

The abnormalities of irradians also become significant in comparison with the normal condition in other species. The grooving of an external ridge takes place normally in *P. islandicus*, right valve, as we have seen. The development of a rib by interpolation in a groove is also typical of *P. islandicus*, left valve. The formation of a small rib on the side of a typically large one is found on the left valve of *P. islandicus*, is the regular thing in *P. australis*, from South Australia,[1] and is also common in other species where the number of rays increases with age. How are we to interpret this correspondence between an abnormality and a normal condition in another species? There was a time when we should not have hesitated to put the phenomenon in the category "reversion." But we have so many instances of parallelism between the abnormal of one species and the normal of a second that we should be cautious in attributing them all to reversion. It seems better to recognize that a physiological potentiality which crops out (as an abnormality) in various species becomes fixed as a normal specific character in one of them.

SUMMARY.

The right or lower valve of *P. irradians* has on the average half a groove more than the upper, because the series of alternating ridges and grooves of the right valve has a prevailing tendency to end in grooves. Of three Long Island localities, the most nearly land-surrounded shows Pectens with the greatest number of rays. The right valve is less variable than the left, a result which agrees with the fact that the right valve of Pectens is generally more archaic than the left. The variation is nearly normal in both valves; more so in the left than in the right valve. The skewness is positive, showing a slight tendency towards an excessive production of the many-rayed individuals, or the selective annihilation of those with few rays. This positive skewness is paralleled by the fact that *P. irradians* seems to be developing towards a larger number of rays. The various abnormalities of Pecten are either explained as

[1] Field Columbian Museum, No. 8430.

self-adjustments to accidents or as sports which represent typical conditions in allied species.

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